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PERENNIAL RAGWEEDS (AMBROSIA) IN MICHIGAN, WITH THE DESCRIPTION OF A NEW, INTERMEDIATE TAXON

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Michigan is a key state for the study of the eastern spread of *Ambrosia coronopifolia* Torrey & Gray, the so-called "western ragweed." Present evidence indicates that what is generally called the "western ragweed," and usually identified as *A. psilostachya* DeCandolle in the literature of allergy and in many botanical manuals, comprises actually a series of closely related but more or less distinguishable types which, for the purposes of this report, will tentatively be treated as species, as was done by Rydberg in 1922. These taxa differ from each other in characters of hairiness, plant habit, distribution, shape of fruit, pollen size, and other characters, although the differences may be in statistical trends. The true or entirely typical *A. psilostachya* apparently does not grow in the central United States. The easternmost outlier of the complex, which is *A. coronopifolia*, is the sole species of ragweed in the central states known to be perennial, i.e., to have underground vegetative reproduction. The investigation to be reported here grew mostly out of our curiosity as to what importance the perennial ragweeds have in forming the ragweed populations in Michigan. We have succeeded in adding a large number of new records to the known range of perennial ragweeds in this state and have compiled considerable new information concerning them.

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Ambrosia coronopifolia is the least abundant generally of the three ragweeds (*A. artemisiifolia*, *A. coronopifolia*, and *A. trifida*) heretofore known in Michigan (Lovell, Mathews, and Sheldon, 1953). It has been reported to be "rare or absent" in the Upper Peninsula of Michigan, and "found occasionally to frequently" in the Lower Peninsula (Buchholtz et al., 1954). There is a question whether the species is native to Michigan at all, and this problem will be considered in some detail below. One of the peculiarities of perennial ragweeds which has been reported earlier is that the period of pollen production differs from that of *A. artemisiifolia* (syn. *A. elatior*), the "common" or "low ragweed," and we attempted to determine whether this was true of the populations in Michigan. We also endeavored to determine in the field whether there were any circumstances indicating differences in ecological responses between the two species.

Quite early in the study it became apparent that the natural variation of *Ambrosia coronopifolia* is fairly extensive; but as more and more populations were examined it turned out that not all the perennial ragweeds in Michigan belong to this species. On the contrary, a perennial species was found to be present that resembled both *A. coronopifolia* and the annual *A. artemisiifolia*. Such a plant, so far as we can determine, has not been described previously. The new ragweed has proved to occur over a large area, with stations in a number of counties; and it has also proved to be able to spread and form extensive populations in a given locality. The discovery of this new form generated comparative field and laboratory studies on all three of these ragweeds, in terms of their vegetative characteristics, their chromosomes, pollen grains, and fruits.

This investigation was carried out by the senior author in the years 1956 and 1957. He was joined by the junior author in the summer of 1957, and the latter added a large number of chromosome and spore studies. We are indebted for assistance to various people, especially J. M. Sheldon and E. W. Hewson, directors of the Project on Atmospheric Pollution, for stimulating this study to be made; Mrs. D. A. Beals, for collecting California ragweeds for comparison; H. H. Bartlett, for the latin diagnosis; R. W. Hanlin, for help on measurements; E. G. Voss, for aid on historical matters; K. L. Jones, for his reading of the manuscript; and the curators of the following herbaria for lending specimens and looking up records: New York Botanical Garden, Michigan State University, University of Michigan, University of Minnesota, University of California (Berkeley), U. S. National Herbarium, and the Gray Herbarium. This report will deal with *Ambrosia coronopifolia* first, and will follow with a discussion of the new, intermediate species.

OCCURRENCE: *Ambrosia coronopifolia* is capable of forming very large populations locally. Because the reproduction takes place largely by vegetative means[2], a given area may be populated by the derivatives of only one or a few original mother plants. "Pure cultures" of a given variant may be distributed over hundreds of square yards, but they are clonal and represent offshoots of a single plant. Usually the spatial distribution of a given clone can be readily recognized because of subtle differences of color, hairiness, size, and shape between the individuals of different clones. Two or more different clones may intermingle more or less intimately but their members remain completely distinguishable. In Mecosta County, for example, numerous plants of a fruiting form with a bright-green color were found completely intermixed with a nearly sterile form with a dull-green color.

The environments in which perennial ragweeds thrive in Michigan are apparently always disturbed sites, the disturbance mostly of artificial nature. The annual species, *A. artemisiifolia*, also grows in such habitats; and where the perennial species occurs, the annual one is almost always near by. The latter is usually unable, however, to invade grassy fields. The annual ragweed is generally confined to open soil, but the perennial species will readily invade adjacent grassy fields and grow competitively with fairly dense field vegetation. In this connection, one of the most interesting occurrences of *A. coronopifolia* and *A. artemisiifolia* growing together was observed on the outskirts of Gaylord, Otsego County; here both species were scattered abundantly along the roadsides, but *A. coronopifolia*

[2] The underground axes of the perennial ragweeds are commonly referred to as "rootstocks" or "rhizomes," but this does not seem to be accurate. The reproductive organs appear to be roots anatomically rather than stems (as was correctly given by Fernald, 1950), and it is hoped that a detailed report on the process of reproduction will be published in the future.

had spread over some sixty square yards of a large, mowed, private lawn, and its pale-green foliage was very conspicuous even though its shoots had been cut to the level of the grass. Only a few, scattered plants of *A. artemisiifolia* were seen in this lawn.

In behavior *A. coronopifolia* is decidedly "weedy" in Michigan, as noted by the earliest writers who mentioned the species in the state. Of the state's collections on which environmental data are recorded, about one-sixth specify that the habitat was along railroads, and one-third say "along roads" or "along highways." Over two-thirds of the collections came from about cities, villages, and settlements. The species can become a locally serious weed in yards and gardens (e.g., around the Interlochen R. R. Station area, and on the outskirts of Frederic and Gaylord). Because of its tendency to form large and dense clones it could provide a local hayfever problem, especially in the weeks before the annual species comes into flower, as will be discussed below.

The soil in which *A. coronopifolia* grows is ordinarily dry, very well drained, and commonly sandy or gravelly. Nearly one-third of the labels on Michigan herbarium specimens use the words "sandy" or "gravelly." The habitats that are found away from roadsides and railway lines are generally clearings, "deserts," open pastures, mowed fields, grass-covered hills, baseball diamonds, and waste ground and dumps. The species evidently can not withstand any great degree of shading; when in wooded areas it will always be discovered on the cleared ground —along open trails, or in more or less exposed, prairie-like spots such as the open sandy and grassy hillsides in jackpine (*Pinus banksiana*) regions.

Although *A. coronopifolia* may be extremely abundant locally, the species must be rated as only frequent to uncommon taking the state in its entirety. In the northern part of the state, i.e., the northern half of the lower peninsula and all of the upper peninsula, it may be found readily by driving along roads and highways, but this impression is misleading with respect to the state flora as a whole, because it is exactly those places where one is likely to drive where the species is most surely to be found. *Ambrosia artemisiifolia* is infinitely more common in the state as a whole. The giant ragweed, *A. trifida,* is locally frequent to common in the southern half of Michigan, but it becomes very rare in most of northern Michigan except around certain towns. Thus, where *A. coronopifolia* is the most common, *A. trifida* is usually rare or absent. In our field surveys, all three species of ragweeds were found growing together only at Cheboygan, Cheboygan Co., and Marquette, Marquette Co., in weedy city lots. *Ambrosia trifida* was considerably less common at these two places than the other ragweeds.

There seems to be a question whether *A. coronopifolia* was originally indigenous in Michigan or not. Fernald (1950) gave the range of this plant (as *A. psilostachya* var. *coronopifolia*) as "Mich. to Sask. and Mont., s. to La., Tex., and Mex.; adv. e. to Quebec, N.S. and N.E." On the contrary, Cronquist in Gleason (1952) circumscribed the range (of *A. psilostachya*) as "Ill. to La., w. to Sask., Ida., Cal., and n. Mexico; introduced eastward," and thus left Michigan out of its presumed original range.

Today *A. coronopifolia* is widespread in Michigan and it has been recorded from forty-three counties, as shown in Figure 1, A. The species extends across the Upper Peninsula down to the middle of the Lower Peninsula. Further southward, i.e., in the bottom half of the Lower Peninsula, the species is frequent only in the western or Lake Michigan side of the state. It is exceedingly rare in the southeastern quarter of the Lower Peninsula at the present time, and we have not succeeded in finding any populations; there is only one record from this part of Michigan.

The earliest definite record of this species in Michigan known to us was in the year 1900, and there are apparently no prior collections[3]. The first mention of perennial ragweeds in the state was in a list published by Daniels (1904) of plants found at Manistee, Manistee Co., that had not been included in Michigan

[3] That it might have been collected as early as September, 1831, by Douglass Houghton, was suspected because of two herbarium sheets so dated and labelled "Fox River of L. Michigan" (MICH). The notion was dispelled, however, by consulting H. R. Schoolcraft's description (1834) of his expedition in 1831. Schoolcraft wrote that "At Galena [Illinois] the exploring party separated, part returning in canoes up the Wisconsin, and part crossing the mine country, over the branches of the Paktolika, and by way of the Blue Mounds, to Fort Winnebago. From this point, Fox River was descended to Green Bay, and the route of the lake coast pursued northward to the straits, and to the Sault of St. Mary." Thus the "Fox River" of Houghton's 1831 collections of *A. coronopifolia* came from the river of that name in Wisconsin, south of Green Bay. It is interesting that Houghton himself (*in* Schoolcraft, op. cit.) gave the locality for various plant species of his report as "Fox River, N.W. Terr.," but did not list this species.

by previous writers. He lists the species under "Weeds" as occurring in "Yard and roadside, Maple Street, near Catholic Cemetery," and a specimen from this collection is deposited in the Michigan State University Herbarium. For the two annual species of ragweeds, *A. artemisiifolia* and *A. trifida*, there are much earlier records: *A. trifida* was taken as early as 1838 by Houghton's survey at White Pigeon, St. Joseph Co. (and there are other collections as early as 1861 and 1869). *Ambrosia artemisiifolia* was obtained in the same year, by the same survey, but in Cass County (MICH).

That *A. coronopifolia* could have been overlooked during the entire nineteenth century seems quite unlikely unless the species was exceedingly rare. Its usually large clones with their characteristic pale foliage are readily noticed in the field. *Ambrosia coronopifolia* was collected considerably earlier in the states to the west (namely Wisconsin, Illinois, South Dakota, and Minnesota) as shown by specimens in the herbaria of the University of Michigan, Michigan State University, and other institutions. Many parts of Michigan, where *A. coronopifolia* now forms a conspicuous element of the vegetation were reasonably well collected by botanists prior to 1900. The region of Douglas Lake (Emmet and Cheboygan Cos.), for example, was examined by a number of botanists during the nineteenth century (Voss, 1956), but none of them found the perennial ragweed.

In 1899, C. K. Dodge completed a flora of St. Clair Co. based on nearly twenty-five years of collecting, but in a list of 1,112 species *A. coronopifolia* was lacking. Four years later he discovered it for the first time in this county. Dodge, who was a very active observer and collector of Michigan flora, and continued his work through the early decades of the present century, evidently concluded that this species was in the process of becoming naturalized. His statements, such as "a weed noted in waste places of Marquette, Negaunee, and Ishpeming . . . becoming frequent" (1918); and "becoming established in cities and villages as a perennial weed" (1921) clearly indicate that he considered the species to be behaving as an adventive.

Professor H. H. Bartlett, another botanist of long experience with the Michigan flora, expressed his opinion recently (1952) as follows: "This is a prairie species that seems to be taking ad-

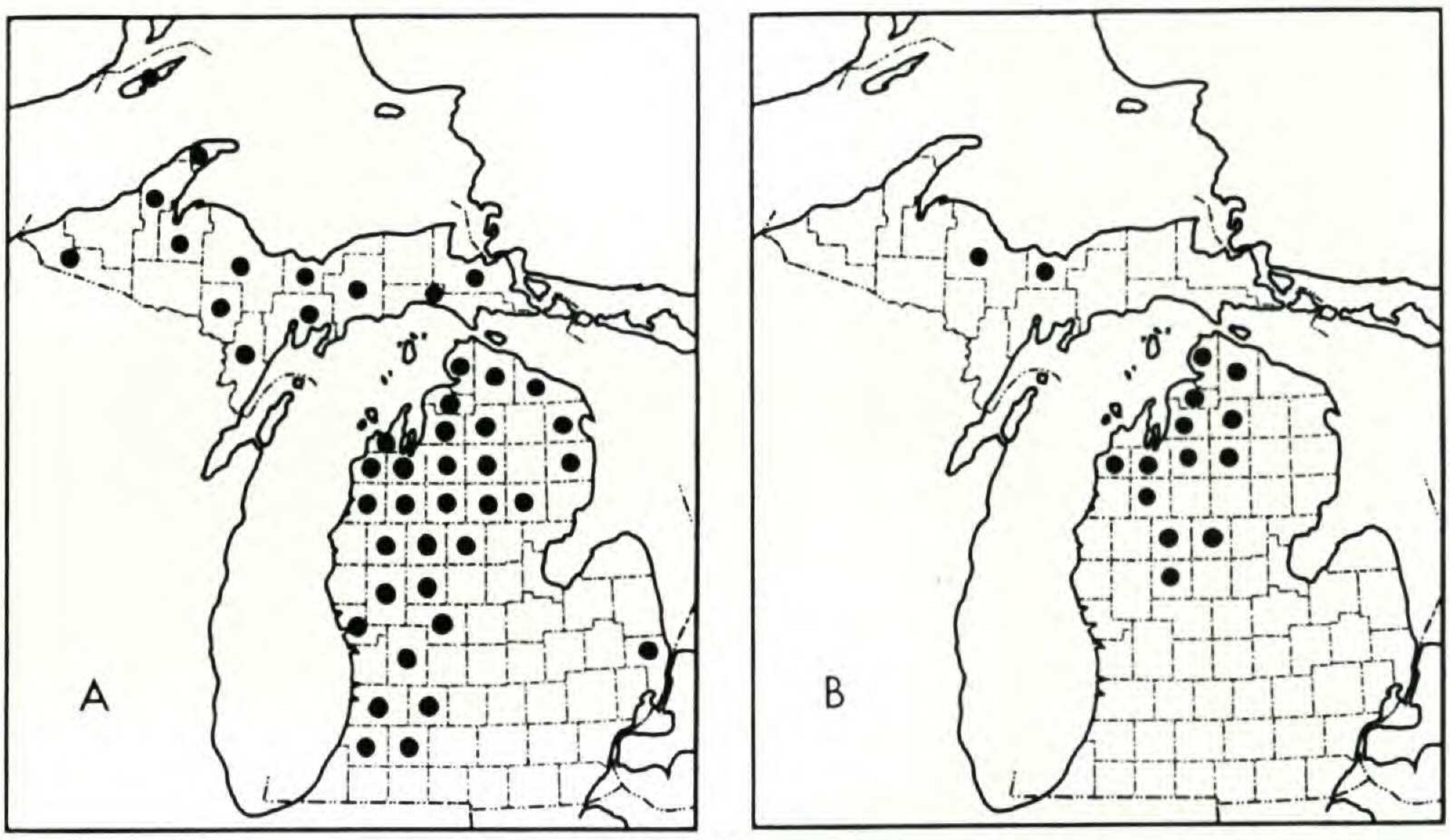

FIG. 1. County distribution maps of perennial ragweeds in Michigan: A. *Ambrosia coronopifolia*. B. *A.* × *intergradiens*. (Base maps courtesy of Cranbrook Institute of Science).

vantage of the clearing of forest and making headway in an eastern invasion fairly well to the north but not in southern Michigan." Observations by him and Dr. C. D. Richards (both botanists allergic to ragweed pollen) on a field trip to the north in 1951 indicated that "north of Gratiot County, Michigan, the amount of ordinary ragweed decreased appreciably, with resultant relief from allergic symptoms." When they reached Emmet Co., they observed that "although we had run beyond the region of greatest abundance of the ubiquitous common species, *Ambrosia artemisiifolia*, we had come into the newly extending range of another, namely *A. psilostachya* [i.e., *A. coronopifolia*]."

All that we can surmise, therefore, is that *A. coronopifolia* has spread since 1900 into a great number of localities in Michigan. It was either very rare and local, or non-existent, in the state prior to that time. It seems not unlikely that the bulk, if not all, of the present-day populations may have been introduced from further west—Minnesota, Wisconsin, and perhaps Illinois—where the species was in all likelihood native and well established. Deam (1940) considered this plant to be a rarity in nearby Indiana and to be introduced there. Moss (1956) has concluded on grounds similar to ours that another species, *A. artemisiifolia*, had been introduced into southeastern Alberta and adjacent

Saskatchewan, and he cites the fact that the earliest collection was in Saskatchewan in 1879.

Surely the development of great railroad lines and innumerable roads and villages and towns over the state of Michigan during the last century has opened the way for active invasion of *A. coronopifolia* into areas where it never before existed. In the course of its spread it has come repeatedly into contact with the abundant and weedy *A. artemisiifolia* which has itself also increased in numbers, and, where the two species have crossed, new types of perennial ragweeds have been generated which combine the characteristics of both, to be discussed below. An enumeration of present county distribution is given in the following list which contains the earliest records for *A. coronopifolia*, the years indicated in parentheses:

Alcona (1957), 1 mi. E. of Mikado, *Wagner 8482* (MICH); Alger (1957), Melstrand, *Wagner 8438* (MICH); Allegan (1950), Ely Lake, *Bazuin 8313* (MSC) also referred to by Kenoyer, 1934; Alpena (1957), Alpena, *Wagner 8483* (MICH); Antrim (1956), W. of Alba, *Wagner 8340* (MICH); Baraga (1950), N. of Baraga, *Richards 4342* (MICH); Barry (ca. 1930), reported by Bazuin, ms.; Benzie (1956), W. side of Co. 669, E. edge of Sect. 25, *Wagner 8334* (MICH); Charlevoix (1957), town of Walloon Lake, *Wagner 8434* (MICH); Cheboygan (1913), Indian Settlement, *Barnum* (UMBS); Chippewa (1935), Sugar Island, *Hermann 7235* (MSC, NY, US); Clare (1957), Meredith, R.3W, T.20N, Sect. 13, *Wagner 8513* (MICH); Crawford (1956), S. border of Frederic, *Wagner 8346* (MICH); Delta (1949), 2 mi. E. of Rapid River, *McVaugh 11170* (MICH, CRANBROOK); Dickinson (1951), 2.4 mi. W. of Norway, *Bartlett & Richards 793* (MICH); Emmet (1921), W. of Pellston, *Ehlers 1817* (MICH, UMBS); Gogebic (1919), 3–4 mi. N.E. Watersmeet, *B. & D. 2779* (MICH); Grand Traverse (1956), Interlochen, *Wagner 8336* (MICH); Houghton (1926), Calumet Water Works, *Wolff 795* (MICH); Kalamazoo (1937), 6 mi. W. of Schoolcraft, *Hanes 3827* (NY); Kalkaska (1956), M-72, just E. of Co. 597, *Wagner 8337* (MICH); Kent (ca. 1930), reported by Bazuin, ms.; Keweenaw (1910), *W. S. Cooper 274* (GH); Lake (1948), 7 mi. W. of Baldwin, *McVaugh 9797* (MICH); Leelanau (1956), E. of Empire, *Wagner 8332* (MICH); Mackinac (1913), Bois Blanc I., *C. K. Dodge* (MICH); Manistee (1900), *F. P. Daniels s. n.* (MSC); Marquette (1916–17), reported by Dodge, 1918, collected along M-28 at Marquette, *Wagner 8440*, in 1957 (MICH); Mecosta (1957), 0.3 mi. N. of Stanwood, *Wagner 8499* (MICH); Menominee (1933), *Grassl 2623* (MICH); Missaukee (1957), Lake City, *Wagner 8475* (MICH); Montcalm (1957), 2 mi. N. of junct. U.S. 131 and M-46, *Wagner 8506* (MICH); Muskegon (1949), Cedar Creek Twp., Sect. 18, *Bourdo 25* (MICH); Newaygo (1916), *Bessey & Darlington 1106* (MSC); Ogemaw (1957), West Branch, *Wagner 8480* (MICH); Osceola (1957), 3 mi. N.W. junction of M-61 and M-115, *Wagner 8500* (MICH); Otsego (1956), S. of Gaylord, *Wagner 8344*

(MICH); Presque Isle (1949), Bearinger Twp., *Marshall 857* (MSC); Roscommon (1919), N. end of Higgins Lake, *Bessey s.n.* (MSC); St. Clair (1903), Port Huron, *C. K. Dodge* (MICH); Schoolcraft (1915), reported by Dodge, 1921; Van Buren (1906), very rare, *Pepoon 944* (MSC); Wexford (1956), juncture M-115 and U.S. 131, *Wagner 8330* (MICH).

PERIODICITY: Wodehouse (1945, table iv) has already indicated that the pollen of "*Ambrosia psilostachya*" precedes that of *A. artemisiifolia* in the atmosphere by two weeks. It was therefore no surprise that field studies of the two species in Michigan revealed the same approximate relationship between *A. coronopifolia* and *A. artemisiifolia* in their morphological development. A total of 338 plants were collected during the period August 3–5, 1956, 234 of *A. coronopifolia* from eight localities in eight counties, and 104 of *A. artemisiifolia* from nine localities in nine counties. These specimens were then measured for length of the staminate spike primordia. In *A. coronopifolia*, 18% of the total branches bore staminate spikes which were over 3 cm. in length, many of these with mature flowers. In *A. artemisiifolia*, a mere 1% of the total bore spikes of such development during the first week of August. In *A. coronopifolia*, only 19% of the total number of branches lacked visible spike primordia, but in *A. artemisiifolia* 64% had no visible primordia. About one week earlier the same year, Professor K. L. Jones reported that on July 27–28, he developed a hay-fever reaction while visiting the city of Cheboygan. Along the estuary there, he discovered a large number of plants of *A. coronopifolia* in anthesis, while the *A. artemisiifolia* was not yet in bloom. The earliest herbarium specimen with flowers in *A. coronopifolia* in Michigan is July 12 (Menominee, C. O. Grassl 2623, 1933, MICH).

VARIATION: Of the three basic ragweed species in Michigan, *A. coronopifolia* seems to be the least variable. The uniformity of any given stand, however, may be misleading, since the individuals are clonal and tend to be derived from one or a few original plants as discussed earlier. The most conspicuous variations include those in leaf form, leaf arrangement, plant habit, and fruit characteristics.

The leaves have been described by Rydberg (1922) as "ovate in outline, pinnatifid, subsessile, or the lower with short winged petioles." The outline may vary, however, as shown in Figure 2

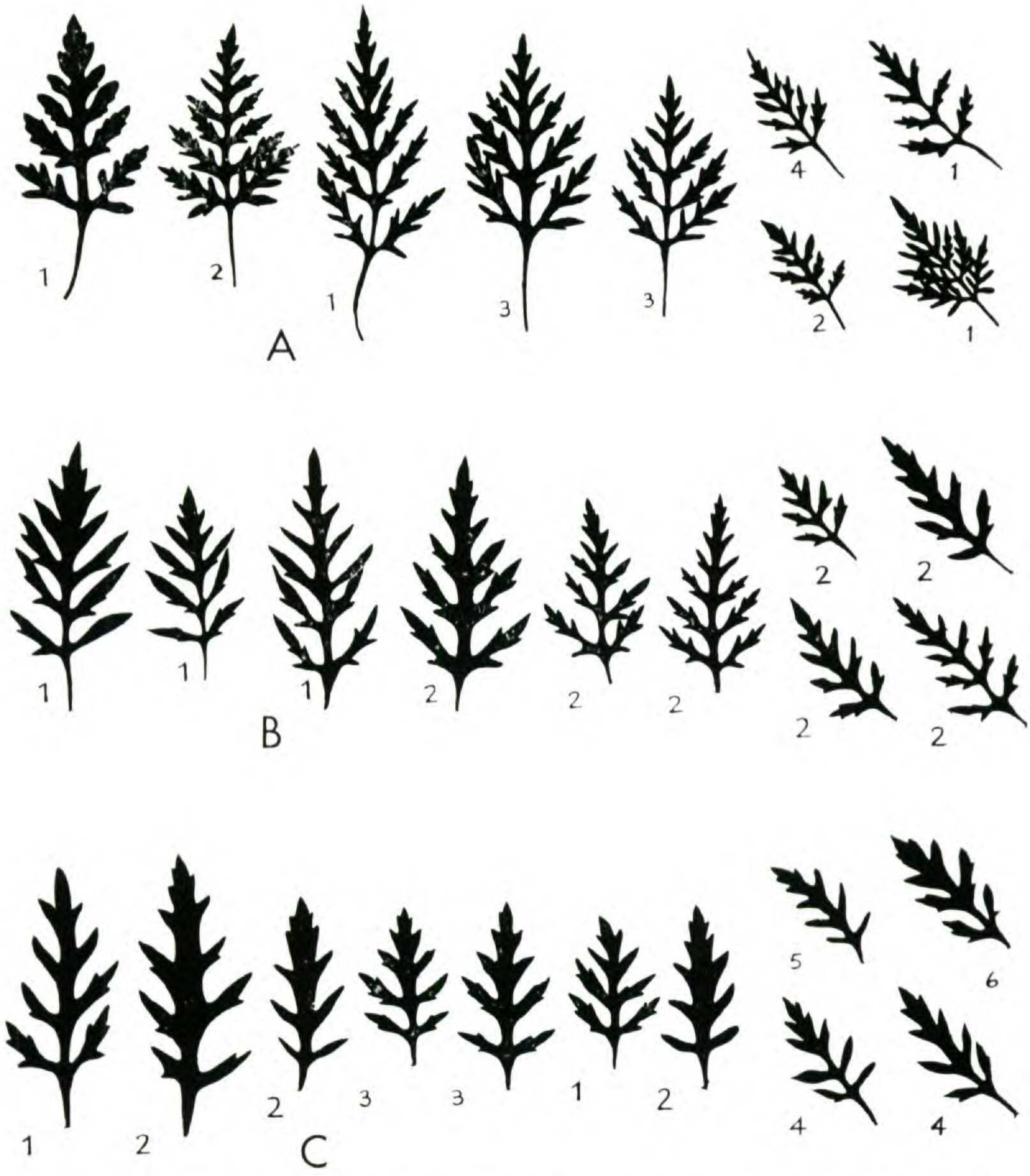

Fig. 2. Outlines of approximately median leaves of moderate-sized plants of ragweeds from Michigan (all petiole bases not complete): A. *Ambrosia artemisiifolia*: 1. Washtenaw Co.; 2 Otsego Co.; 3. Benzie Co.; 4. Crawford Co. B. *A.* × *intergradiens*: 1. Crawford Co.; 2. Benzie Co. C. *A. coronopifolia*: 1. Benzie Co.; 2. Grand Traverse Co.; 3. Leelanau Co.; 4. Antrim Co.; 5. Otsego Co.; 6. Kalkaska Co.

(e.g., 2 vs. 3) from approximately lanceolate to deltoid. Extremely large leaves (not figured) from plants growing under luxuriant conditions may approach in outline and cutting the much smaller, typical leaves of *A. artemisiifolia* growing under normal conditions. The length of the petiole diminishes from the basal to the median leaves, varying from obviously petiolate to sessile, making comparisons quite difficult from collection to collection unless leaf position is taken into consideration. The dissection of the leaves ranges from coarsely lobed to nearly bipinnatifid. In the least dissected extreme the leaf-blades are long-ovate and the sinuses so shallow that they extend only one-third to one-half of the way from the blade margin to the midrib. The other extreme is represented by triangular leaf-blades cut seven- to nine-tenths of the way to the rachis, resembling in leaf outline *A. artemisiifolia* forms except for the relative length of the petiole. The blade/petiole ratio of median leaves averages 4.2 but varies from 3.1 to 8.0.

Occasional specimens of *A. artemisiifolia* are collected, especially in southern Michigan, which resemble *A. coronopifolia* in foliar characters. Generally, however, the leaves of the latter may be distinguished by the following ensemble of differences, some of them subtle and not readily evident on the herbarium sheet: (a) thicker leaf texture; (b) harsher, more appressed hairs; (c) paler green color; (d) fewer lobes and segments; (e) broader midrib wing; (f) shorter petiole; and (g) narrower blade outline. All these characters tend to overlap individually to some extent between the two taxa, and they must, therefore, be considered together in making identifications.

Leaf arrangement in *Ambrosia coronopifolia* does not differ basically from that of the other ragweeds. Depending on size of plant, the lower four to nine leaf pairs are opposite, but the leaves above and especially those from the axils of which the staminate inflorescences arise tend to be subopposite to alternate. At Interlochen, Grand Traverse Co., however, there is at least one large clone, growing with clones of the ordinary opposite-leaved form, in which the leaves are all whorled, with three leaves per node. In this "leafy" form, the spacing of the nodes is like that in the typical form, and in the upper part of the plants the whorled condition gives way to the usual alternate-leaved state.

In habit the plant is usually a simple leafy axis. The vast majority of plants in typical exposed situations on sterile soil along roadsides and railways have simple axes with only a single terminal staminate spike or with one or a few laterals in the upper fourth of the plant. A few more lateral branches may tend to develop from axillary buds as the season progresses, thus spreading the potential flowering time. If the main stem of a plant is cut off or otherwise damaged during the first half of the summer, a short, "bushy" specimen will result, numerous branches arising from the base of the stem.

The only profusely branched forms that are not the result of injury are the giant plants found in unusually rich environments. This large form was found at the edge of a vacant lot in Alpena, Alpena Co. (*Wagner 8483*) and on a farm near the juncture of highways M-72 and Co. 597 in Kalkaska Co. (*8337*). At the latter site, the normal form with few branches occurred in fields and had spread into open soil in a cultivated truck garden where giant plants up to 70 cm. tall formed, bearing in some cases over 30 large and well developed staminate spikes with numerous coarse vegetative branches arising from near the base. These were very likely stimulated to grow and branch by the unusually rich soil conditions in the truck garden where they were free of competition. In growth habit they resembled the large, branching plants characteristic of true *Ambrosia psilostachya* as it grows in California, rather than the simpler forms typical of *A. coronopifolia* as it occurs in the Great Lakes area.

The morphology and maturation of fruits varies to some extent from clone to clone. It is not at all uncommon to find populations of *A. coronopifolia* in which only a small number of fruits have been produced. Such populations may co-exist side by side with others which have fully developed fruiting. Morphologically the fruits of *A. coronopifolia* usually have very short lateral processes or none at all so that they become, in the extreme form, entirely rounded at the top except for the beak. One striking population at Yuma, Wexford Co. (8497a), however, has fruits with rather conspicuous processes, suggesting the fruits of *A. artemisiifolia.*

POLLEN GRAINS: The pollen grains of *Ambrosia coronopifolia* were studied in terms of size, and presence or absence of protoplasts. To measure diameters, anthers were removed from herbarium specimens, placed in 75% aqueous ethyl alcohol on a microscope slide and glycerine jelly containing acid fuchsin was added. The measurements were made of the widest diameters of 20 grains for each collection. No broken or collapsed grains were measured. To estimate the number of inviable grains, the technique was to crush dried anthers in aceto-carmine and to

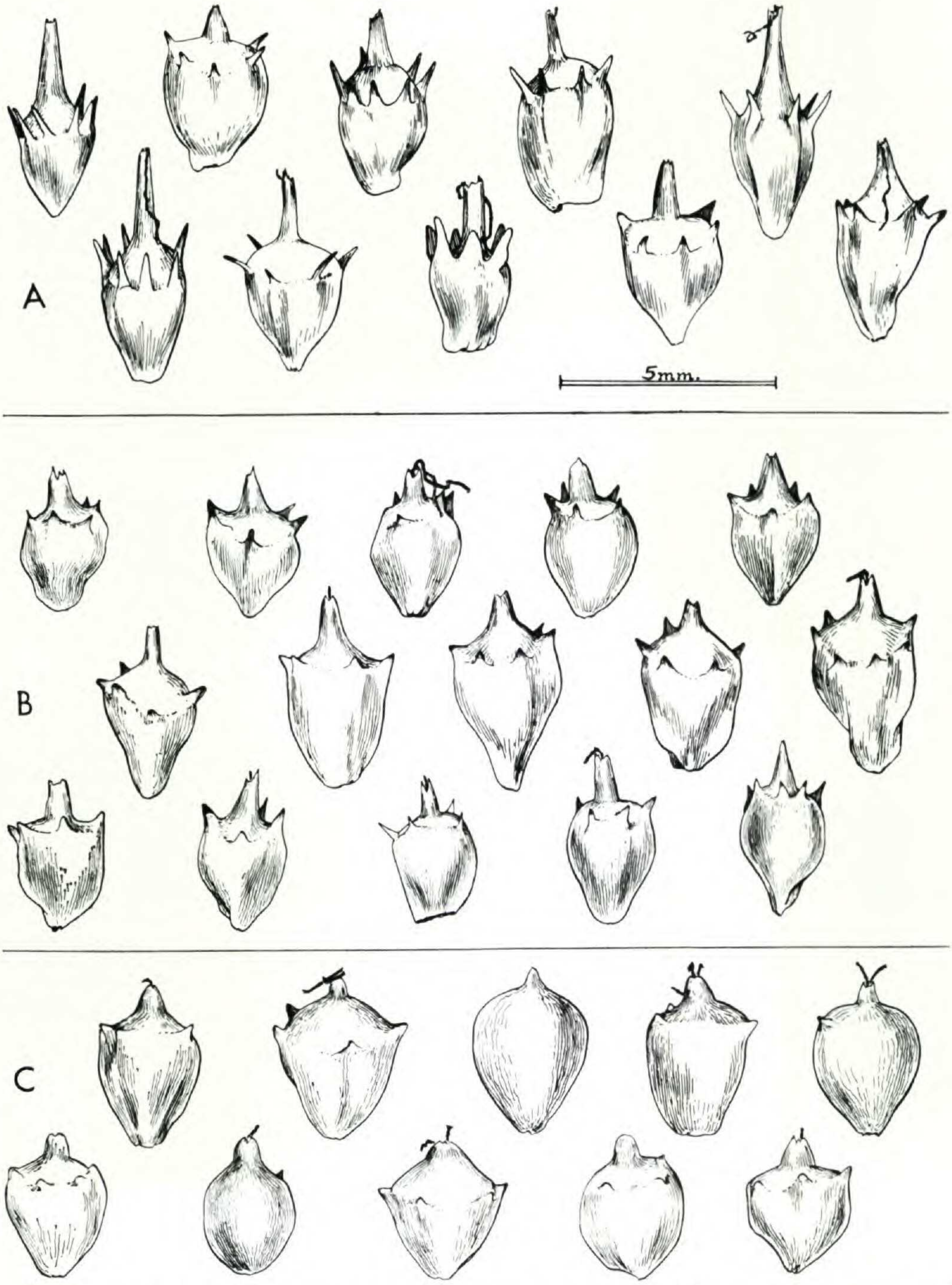

FIG. 3. Fruits of ragweeds collected near Stanwood, Mecosta Co., Mich., September 28, 1957 (specimens drawn without trichomes): A. *Ambrosia artemisiifolia* (from several plants). B. *A.* × *intergradiens* (each horizontal row from a different clone). C. *A. coronopifolia* (each row from a different clone).

heat the freed pollen grains until all the protoplasts became stained. Those grains in which no protoplasts were evident by staining were counted and compared with those in which the protoplasts did stain. Approximately 1000 grains were recorded

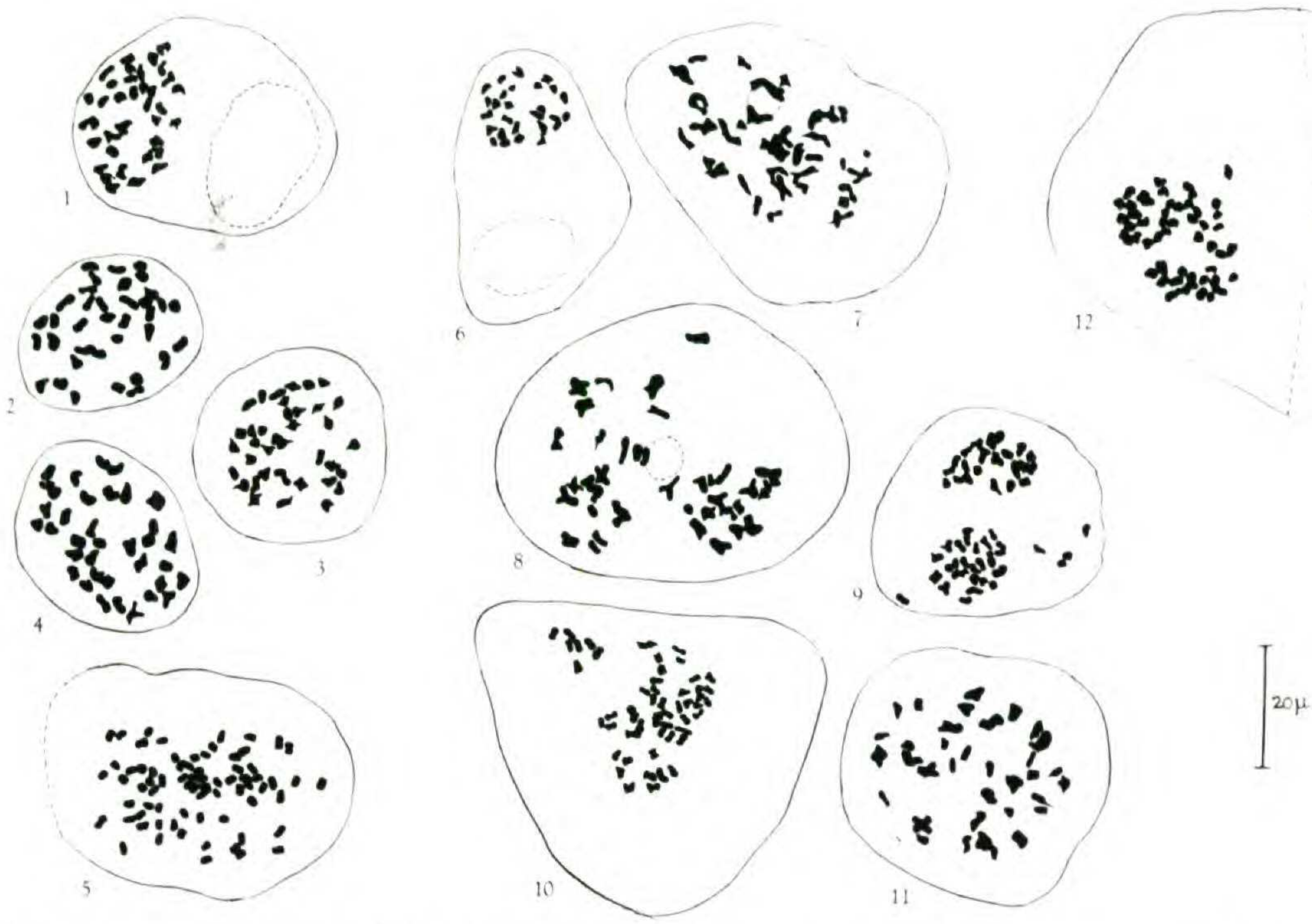

Fig. 4. Chromosomes of Michigan Ambrosia. 1–5. *A. coronopifolia*, $2n = 72$: 1, Antrim Co., metaphase II, 8340; 2, Emmet Co., metaphase I, 8446; 3, Benzie Co., metaphase I, 8334; 4, Mackinac Co., metaphase I, 8435; 5, Alger Co., mitotic metaphase, 8438-bl. 6–11. *A.* × *intergradiens*, $2n = 54$: 6, 9, Emmet Co., metaphase II, 8445; 7, 8, Emmet Co., late prophase, 8445; 10, Alger Co., mitotic metaphase, 8438–2; 11, Emmet Co., prophase I, 8445. 12. *A. psilostachya*, $2n =$ ca. 108, Los Angeles Co., California, metaphase II, D. A. Beals.

in this way with mechanical counters, and the results expressed as percentage abortive grains of the total.

The average pollen diameter of 11 collections of *Ambrosia coronopifolia* is 20.5 microns, with a range in individual grains of 17.6 to 25.0, and a standard deviation of 1.05. An average of 22.6% of the pollen grains from 11 collections appeared to lack protoplasts, with a range from 5 to 72%. Comparison of these values with those of the other ragweeds involved in this report is shown in Table 1, and will be discussed below.

CHROMOSOMES: To determine chromosome numbers, specimens were fixed in Newcomer's fluid (Newcomer, 1953). For meiotic observations, whole young staminate spikes were placed in the fixative after removal from plants grown in the University of Michigan Botanical Gardens (August, 1956), and from the wild (July, 1957). At the time of examination, individual involucres were removed, the florets dissected out, and the anthers carefully removed and crushed in aceto-carmine stain on a microscope slide. The pollen mother cells were thus extruded, and were then squashed in the ordinary way. For somatic observations, root tips were removed from greenhouse plants and pre-treated before fixation in a saturated cool solution of paradichlorobenzene and kept in a 40° cold-room for 3–5 hours to shorten the chromosomes. The roots were then fixed and squashed. Division figures were drawn using the camera lucida.

As stated in a preliminary report based on observations made during 1956 by the senior author (Wagner, 1957), there are 36 bivalents in meiotic metaphase, all of approximately the same size. This number has been confirmed by studies made in 1957 by the junior author, and also by the report, based presumably on the same species, of Mulligan (1957). Meiosis in *Ambrosia coronopifolia* is evidently regular, and the division figures of all stages appear to be normal (Figure 4, 1–5). Counts of $n = 36$ or approximately that number were made in meiosis of the following collections: Benzie Co., 8334; Antrim Co., 8340; Emmet Co., 8430; Mackinac Co., 8435; and 8444; and Marquette Co.; 8439. Counts of $2n = 72$ or near that number were made in mitosis in the following collections: Kalkaska Co., 8337; Grand Traverse Co., 8336; Benzie Co., 8334; Alger Co., 8438bl; and Emmet Co., 8444-1. Representative specimens of all these collections are on deposit in the University of Michigan Herbarium. The collections from which the majority of meiotic numbers were determined were collected mainly on July 19, 20, and 21, 1957.

INTERMEDIATE PERENNIAL RAGWEED: The second type of perennial ragweed in Michigan is easily overlooked by the collector because of its resemblances both to *Ambrosia coronopifolia* and the annual *A. artemisiifolia*. In all respects, this plant is an intermediate between these two species, and it will therefore be described as a hybrid taxon, *A.* × *intergradiens*[4]. The major characters of the new perennial ragweed are summarized in Table 1, in comparison with its relatives. In its habitat it is generally found with the two other ragweeds, but

[4] *Ambrosia* × *intergradiens* Wagner, hybr. nov. Perennis, multiplicatione vegetative colonias uniformes formans sed inter se multiformes. *Ambrosiae coronopifoliae* similis sed differt plerumque pilis numerosis valde divergentibus in caule primario, foliis plus dissectis, tenuioribus, petiolis longioribus, chromosomatibus ($2n$) 54, divisione meiotica irregulari. Communis in locis dispersis ruderalibus michiganensibus borealibus cum *A. artemisiifolia* et *A. coronopifolia*.

Table I. A comparison of three ragweeds in Michigan.

	artemisiifolia	× *intergradiens*	*coronopifolia*
Duration	Annual	Perennial	Perennial
Petiole length (cm.) (ca. 30 median lvs.)	1.5 (0.3–3.0)	1.0 (0.5–1.7)	0.9 (0.5–1.4)
Number of projections on basal segment pair (ca. 30 median lvs.)	9.0 (0–22)	5.8 (2–10)	2.2 (0–10)
Narrowest rachis wing width between two basal segment pairs. (ca. 30 median lvs.)	1.4 (1.0–2.0)	2.4 (1.5–3.5)	3.1 (2.0–5.0)
Indument of main stem and petioles (subjective judgment)	Sparse and spreading (except f. *villosa*)	Mostly denser & spreading.	Denser and appressed.
No. pistillate fls./cluster	5.4 (2–15)	3.1 (1–8)	1.2 (1–3)
Per cent good fruits/cluster	77	16	55
Terminal beak length of fruit (mm.)	1.2 (0.8–2.0)	0.9 (0.8–1.0)	0.6 (0.5–0.8)
Length of "spines" (mm.)	0.5 (0.2–0.8)	0.4 (0.2–0.6)	0.2 (0.0–0.5)
Per cent abortive pollen per collection	16.0 (3–44) (9 collections)	54.9 (42–83) (12 collections)	22.6 (5–72) (11 collections)
Pollen grain diameter: over-all range (microns)	14.3–20.8	16.6–29.6	17.6–25.0
Pollen grain diameter: averages (microns)	17.6 (16.3–19.7)	21.8 (20.4–23.6)	20.5 (19.9–22.2)
Pollen grain diameter: standard deviation	0.79 (0.58–0.94)	2.30 (1.36–3.22)	1.05 (0.72–1.37)
Chromosome number ($2n$)	36	54	72
Meiotic metaphase	Regular	Irregular	Regular

this is not always so. For collectors in general it is probably most profitable to compare the new plant with the other perennial species, *A. coronopifolia. Ambrosia* × *intergradiens* may be distinguished from the latter by its more spreading, more delicate hairs on the stem axis, these usually more abundant. The whole plant of the intermediate is slightly greener (not glaucous). Corresponding leaves tend to be more divided and they have narrower wings between the pairs of lobes. Corresponding leaves (i.e., those in like position on plants of approximately equal size) will also tend to have slightly longer and narrower petioles. If the fruits have matured, the lateral processes and the beak will be more strongly developed than in *A. coronopifolia* so that the fruit is more suggestive of that in *A. artemisiifolia.*

The hybrid perennial ragweed has turned out to be surprisingly numerous in Michigan. In 1956 and 1957 it is estimated that between forty and fifty different populations, large and small, have been discovered. These were found in over twenty localities in fifteen counties. All collections in the following list were made by the senior author with the help of others, especially J. A. Churchill, R. F. Blasdell, and P. J. Neihaus. Unless otherwise indicated, both parental ragweeds were present at each station listed:

Alger, weedy edges of roads at Munising Falls, Munising, *8438–2*; Antrim, no parents within at least 100 yds., grassy plains along U.S. 131, 1.2 mi N. of county line, Sect. 31, R.6W, T.29N, *8491*; Benzie, on steep road-banks, W. side of Co. 669, E. edge of Sect. 25, R.14W, T.26N, *8335*; in overgrown vacant lot, Bendon, Sect. 23, T.26N, R.13W, *8493*; Charlevoix, vacant lot in town of Walloon Lake, *8485*; along R.R. tracks in Boyne City, *8487*; Cheboygan, vacant lots, Cheboygan, *8434*; Clare, Meredith, R.3W, T.20N, Sect. 13, *8513*; Crawford, lawns, gardens, fencerows, S. border of Frederic, *8348*; gardens and roadsides behind P.O., *8448*; Emmet, sandy vacant lot by Greyhound Bus Station, Mackinaw City, *8444–2*; open grassy places along R.R. tracks, Pellston, *8445*; Grand Traverse, one or both parents present, in 3 places—(#1) in sandy lot near Elementary School, an all-pistillate clone, (#2) just S. of bridge over Little Betsey Creek, and (#3) by the R.R. Station, Interlochen, *8473*; only *A. artemisiifolia* present, along railroad, 0.6 mi. W. of Grawn, Sect. 12, R.12W, T.26N, *8492*; Kalkaska, weedy fields at intersection of U.S. 131, 1.5 mi. S. of Co. line, Sect. 2, R.7W, T.28N, *8488X*; Marquette, both parents plus *A. trifida* present, vacant lot along M-28, Marquette, *8443a* and *8443b*; Mecosta, prairie-like fields, hybrids in sandy, more or less shaded, areas, 0.3 mi. N. of Stanwood on U.S. 131, *8498*; Osceola, only *A. artemisiifolia* seen, grassy fields near R.R. Station, Marion, *8429*; Otsego, 1.2 m. N.N.W. of Vanderbilt on M-27, *8515*; Wexford, grassy fields at junction of M-115 and U.S. 131, *8474*; along R.R. tracks, Yuma, Sect. 34, R.12W, T.23N, *8496a*.

The different intermediates are quite variable among themselves, and it is conceivable that there is some degree of introgression involved in the formation of *Ambrosia* × *intergradiens*. In general, however, we have assumed that we are dealing with F_1 hybrids which have become established and by means of their perennial habit and reproductive method have been able to form more or less large populations. It is interesting to note that *A.* × *intergradiens* is occasionally found with only one parent in the immediate neighborhood of the colony. At one place (Antrim Co.), in fact, we discovered a large population where careful searching failed to reveal either parent within at least 100 yards. The hybrid has been found to invade plowed fields (Otsego Co.), gardens (Crawford Co.), and plantations of pine trees (Benzie and Mecosta Cos.). The best localities for locating large populations are in grassy places along railroad tracks and sandy roads in and around towns and villages. Disturbed areas where both *A. coronopifolia* and *A. artemisiifolia* occur in a large mixture are almost sure to reveal at least one or a few populations of *A.* × *intergradiens*. Further field studies of Michigan weeds will unquestionably yield many more populations of the new ragweed (once its characteristics are recognized), judging from the readiness with which we have found it to date.

The major variations of *A.* × *intergradiens* include degree of hairiness and the size of the plant. The former is probably genetically controlled, and is perhaps determined more by inheritance from the annual ragweed, *A. artemisiifolia*, than the other parent. This is suggested by the fact that *A. artemisiifolia* is strongly variable in hairiness, and the form *villosa* Fern. & Grisc. is common throughout this area, contrasting by its dense, spreading-villous indument with the ordinary form. *Ambrosia coronopifolia* does not vary nearly so much in this respect. The size (i.e., height and number of branches) of the plant, on the other hand, is probably controlled mainly by the environment:

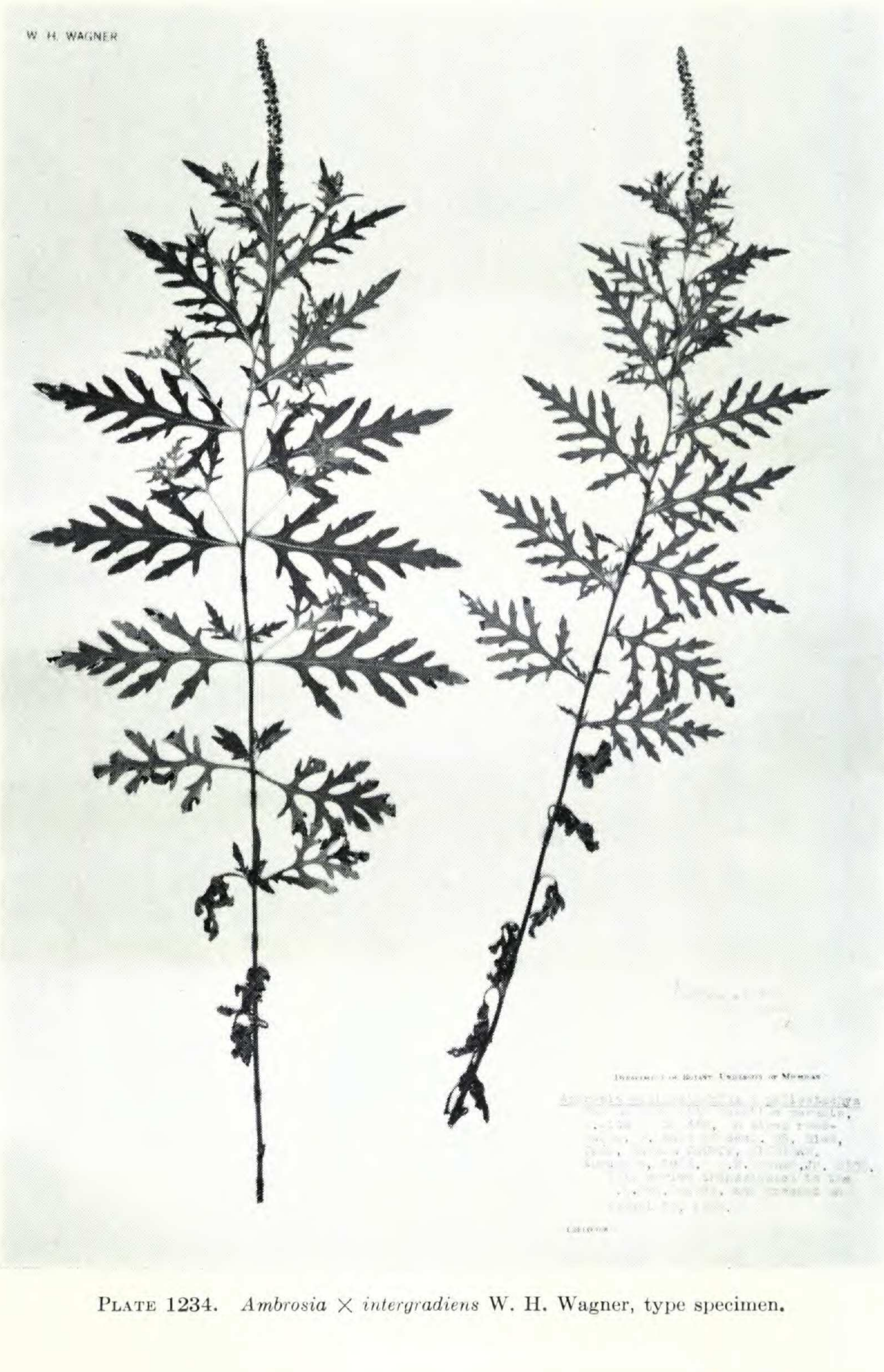

PLATE 1234. *Ambrosia* × *intergradiens* W. H. Wagner, type specimen.

those growing in completely exposed sites tend to be smaller and to have a simple form with only one terminal, staminate raceme (Pellston, R. R. tracks, Emmet Co., 8445); those growing in more or less shady and damper sites tend to be larger and more "bushy" and to have numerous staminate racemes branching out below the terminal one (from near Stanwood, at edges of pine plantation, Mecosta Co., 8509–5).

One of the most curious variants of *Ambrosia* × *intergradiens* was found at Interlochen, Grand Traverse Co. (8473–1). An entire clone was observed to comprise pistillate plants only. The pistillate flowers of these plants are borne in racemes in a manner similar to that of normal, staminate involucres in typical plants. The all-pistillate condition has been well known previously in a variant of *A. artemisiifolia*, which, like the foregoing, bears no staminate flowers at all (Jones, 1936, fig. 6), and which is found with the normal type and intermediates throughout Michigan. The all-pistillate condition is unknown, however, in *A. coronopifolia*, which, so far as is known, always comprises plants of the normal, bisexual type with axillary pistillate flowers and terminal racemes of staminate flower clusters. It seems entirely possible, therefore, that the pistillate intermediate population at Interlochen arose as hybrid in which the female parent was the pistillate form of *A. artemisiifolia*. Jones (1943) succeeded in crossing another ragweed, *A. trifida*, which is, like *A. coronopifolia*, a strictly monoecious species, with the pistillate form of *A. artemisiifolia* and showed that the progeny contained, in addition to monoecious and intergrading forms, the all-pistillate form as well.

In 1910, Rydberg described a plant, *Ambrosia media*, as resembling *A. coronopifolia* in leaf shape. He wrote that "Otherwise, the plant is more closely related to *A. elatior* and *A. artemisiifolia* [which he regarded as separate species], the root being annual and the fruit spiny." Our examination of the type specimen of *A. media*, which was lent to us through the courtesy of Dr. Keck of the New York Botanical Garden, shows that the plant in question is the coarsely lobed form of *A. artemisiifolia*, a form not uncommon as a variant in the populations of this species in southern Michigan. S. F. Blake reduced this plant to synonymy under *A. artemisiifolia* (1925). We further checked the pollen grains of the type specimen and found that the average pollen size is 19.0 microns, the total range from 14.7 to 21.0, and the standard deviation 0.95. The good grains in a sample of 1009 grains formed 79% of the total. Comparison with Table 1 will show that these figures are well within the ranges characteristic of *A. artemisiifolia* and not of *A.* × *intergradiens.*

FRUITS: For comparison of mature fruits of *Ambrosia* × *intergradiens* and its presumed parents, a field study was made on September 28, 1957, north of Stanwood, Mecosta County. In the prairie-like, rolling fields and roadsides there, all three taxa are common, and are readily compared as their fruits are fully developed at this season. In general, those of the parents may be immediately differentiated: those of *A. artemisiifolia* have terminal beaks twice as long on the average (1.2 mm.) as those of *A. coronopifolia* (av. 0.6 mm.). The lateral processes or "spines" of *A. artemisiifolia* average 0.5 mm. in length, while those of *A. coronopifolia* average 0.2 mm. and are commonly absent altogether in the latter as shown in Figure 3, C. There is, however, some variation and overlap as the specimens figured reveal. Any large collection of fruits of *A. artemisiifolia* in Michigan will show some individuals with very short lateral processes; and, as described earlier, a variant of *A. coronopifolia* exists (Yuma, Wexford Co., 8497a) in which the processes on the fruits are unusually well developed. *Ambrosia* × *intergradiens* is intermediate between the two other taxa in fruit morphology (see Table I) and the rather well developed beaks and spines provide a valuable additional character with which to distinguish the new taxon from *A. coronopifolia* in late summer and fall.

The pistillate flowers of *A. artemisiifolia* tend to occur in clusters of five or six in the axils of the upper leaves, but those of *A. coronopifolia* tend to be solitary (as determined from an average of 100 pistillate inflorescences for each species). The average number of flowers in inflorescences of *A.* × *intergradiens* is intermediate, i.e., averaging three flowers. The percentage of fruits which actually enlarge and mature differs considerably in the three taxa: In *A. artemisiifolia,* a total of 541 pistillate flowers counted yielded 415 approximately full-sized fruits, a proportion of 77%. In the plants identified as *A. coronopifolia,* a total of 118 flowers formed only 66 fruits, i.e., 55%[5]. In the hybrid taxon it was very low—of the 280 flowers counted, only 34 had expanded into normal-appearing fruits, only 16%. *Ambrosia* × *intergradiens* thus shows morphologically a high degree of sterility, a condition suggested also by the percentage of bad pollen grains and by the irregular meiotic process to be described below.

It is interesting to note that the clone of wholly pistillate plants of *A.* × *intergradiens* discovered at Interlochen, Grand Traverse Co., failed entirely to set fruits, and repeated collections made during September and October, 1957, of many pistillate spikes revealed not a single fully formed fruit.

POLLEN GRAINS: Following the same technique described above, the average pollen diameter of 12 collections of *A.* × *intergradiens* was determined as 21.8 microns, the total range of individual grains from 16.6 to 29.6. That the pollen grains of the intermediate ragweed turned out to average larger than those of *A. coronopifolia* was surprising, in view of their respective chromosome complements which would lead one to expect the reverse relationship. However, the variation in size of the pollen grains of the intermediate proved to be considerably greater than that of either of the parental ragweeds, including *A. coronopifolia*, and the standard deviation was 2.30 microns for the former and 1.05 for the latter.

Although two of the collections of *A. coronopifolia* revealed a high percentage of non-staining pollen grains (one with 33% and one with 72%), most showed a low percentage and the average of 11 collections was 22.6%. On the contrary, *all* of the collections of *A.* × *intergradiens* had high percentages of abortive grains. The mean of all the collections examined was 54.9% bad grains, the lowest single collection 42% and the highest 83%. These data on abortive pollen and pollen diameters are summarized in Table I, along with similar facts concerning *A. artemisiifolia* for comparison.

[5] If our figures are at all representative for the species as a whole, then *A. artemisiifolia* with its much larger number of pistillate flowers and greater average production of fruit per head has well over six times the reproductive potential by seeds as *A. coronopifolia*. Actually the difference is probably even greater because of the tendency for more axils to form pistillate inflorescences in *A. artemisiifolia*. Thus the annual species which relies entirely on seeds for survival, (so far as we know) shows a striking difference in seed production from the perennial ragweed which relies on its ability to remain alive from year to year and its ability to propagate itself by underground roots.

CHROMOSOMES: Meiosis in the intermediate ragweed shows conspicuous irregularities. First metaphase is characterized by univalents, bivalents, and trivalents, and first anaphase commonly shows lagging of chromosomes. The determination of units from ten well-spread sporocytes from five collections averaged 14.5 univalents (range: 8–19), 15.1 bivalents (range: 11–20), and 2.5 trivalents (0–4). The average total number of units was 32.1 (range: 22–38). A rough explanation for the average pairing behavior might be suggested as follows: There are 54 chromosomes present, 18 from *A. artemisiifolia* and 36 from *A. coronopifolia*. Assuming a fairly high degree of homology between chromosomes of the parents, it then appears that 15 of the chromosomes of *A. artemisiifolia* and 15 of *A. coronopifolia* tend, on the average, to form pairs. The remaining three chromosomes of *A. artemisiifolia* would form trivalent configurations with six chromosomes of *A. coronopifolia*, leaving a residue of 15 univalents of the latter. The situation, however, is very much more variable from cell to cell than such an idealized "average" behavior would indicate.

The lagging that commonly occurs in the chromosomes of first anaphase result in the exclusion of up to as many as four chromosomes from the second metaphase division figures, so that they lie off the respective equatorial planes, as shown in figure 4, 9. At second anaphase, as many as ten chromosomes have been seen lying separate in the cytoplasm, and even after the nuclear membrane is formed, chromosomes may remain unassimilated. As the pollen grains mature, these chromosomes apparently disappear. In material of the intermediate plant from Pellston, Emmet Co., a sample of 171 division figures showing second anaphase had 55% of the figures with excluded chromosomes. The remaining 45% appeared to have normal second anaphase figures[6]. In contrast, in material of *A. coronopifolia* taken at the same time and place, a sample of 39 figures showed all normal second anaphases.

Root tip squashes from three localities of the intermediate ragweed confirm $2n = 54$ chromosomes, as would be expected

[6] Avers, C. J. (Genetics **39**: 117–126, 1953) has suggested a mechanism in Aster whereby triploids produce fertile pollen by means of a double equational division of the univalents. No evidence of such a mechanism has been observed in the present study, but this is a possible explanation of the relatively high percentage of normal-appearing second anaphase figures.

from the known genomes of the putative parents, *A. artemisiifolia* with $2n = 36$ (Jones 1943; Yuasa 1956), and *A. coronopifolia* with $2n = 72$. These localities were in Benzie Co. (8335); Crawford Co. (8348); and Alger Co. (8438–2). Irregular meiotic behavior was observed in the Benzie Co. and Crawford Co. materials, as well as Osceola Co. (8429), Emmet Co. (8445), and other Crawford Co. collections (8448).

DISCUSSION: As botanists did not find *Ambrosia coronopifolia* in Michigan until 1900 we may assume that perennial ragweeds were probably introduced into the state sometime prior to the turn of the century. It should be pointed out, however, that the question of "introduced" vs. "indigenous" may be a vexing one when weeds are involved. Our concepts of these terms do not ordinarily admit of degrees (such as "introduced in part," or "mainly introduced"). With regard to our perennial ragweeds, it seems entirely plausible that from time to time, over thousands of years, small "extra-territorial" emigrations from the home range into Michigan took place. Many, if not all, of these probably died out. However, now—with railroad and highway systems, and myriad artificially disturbed habitats, the species can readily migrate into Michigan along definite pathways from the states further west. So even if the species *had* been present, though extremely rare, prior to 1900, the bulk of present populations may very well have immigrated from further west. Certainly over its present range in the state, the perennial ragweed will have to be interpreted as "mainly introduced." There is no positive evidence to date, in fact, to indicate that it was ever native at all.

When Michigan in its entirety is considered, *A. coronopifolia* must be treated as only frequent to uncommon; but its ability to "take over" large areas locally where the habitat is appropriate make it nevertheless a potential hayfever problem in its restricted territories. Its habit of congregating its populations around settlements make its hayfever significance out of proportion to its over-all abundance. The annual species, *A. artemisiifolia*, will in general much outweigh its allergic importance because of greater numbers. But in the two weeks prior to flowering in annual ragweed, the perennial species may become a local problem to allergic persons.

The hybrid perennial ragweed has turned out to be remarkably common in appropriate localities. If it had been found only once or several times in this investigation it would have been designated only by formula. The intermediate has been given a taxonomic binomial, *Ambrosia* × *intergradiens*, because of a belief that any natural hybrid which comes to form many individuals of importance in the community, whether by sexual means (e.g., as allopolyploids) or by asexual means (e.g., by underground reproductive axes, as in this instance) or both, should be so named. Perhaps other ragweed hybrids (e.g., *A.* × *helenae* Rouleau, an extremely rare plant in Michigan) are formed *de novo* in nature as frequently as *A.* × *intergradiens*, but none of the others, to our knowledge, compare in abundance to the present one which is self-perpetuating and builds up large local populations through the years.

Now that *A.* × *intergradiens* has been distinguished among the populations of perennial ragweeds in Michigan, collectors may be urged to look for it in other states (e.g., Illinois, Minnesota, and Wisconsin) where the two parental species intermingle. The characteristics of the new ragweed are subtle ones, it is true, and they are hard to perceive on casual inspection in the field; but the description and figures given above should suffice for its recognition.

The sizes of pollen grains reported here for the plant commonly referred to as "western ragweed" in the Great Lakes states differ from the previous reports. Wodehouse (1928, 1945) gave the diameter of pollen grains of "*A. psilostachya*" as 23.4 (22.0–27.4) microns. His measurements evidently refer not to our plant but to other taxa in the complex. Pollen grains in *A. coronopifolia* as defined here measure 20.5 microns in diameter on the average. Our own measurements of *A. psilostachya* from California (Solano Co., Heiser 1966; San Diego Co., Alderson s.n.; Colusa Co., Chandler s.n.; Stanislaus Co., Hoover 165; Los Angeles Co., Wolf 4241; and San Luis Obispo Co., Summers s.n.—MICH and UC) gave an average diameter of 23.0 microns, the range 20.0–25.6. There is a correlation of pollen grain diameter with chromosome numbers. Previous studies of chromosomes in the genus *Ambrosia* indicate that the X number is 12, 17, or 18 (Darlington & Wylie, 1955). Jones (1933, 1943) showed the chromosome number in *A. artemisiifolia* (as *A. elatior*) to be $n = 18$; in *A. bidentata*, $n = 17$; and in *A. trifida*, $n = 12$. Of these species the first is most obviously related to the perennial forms under discussion here, and the number of $n = 36$ determined by us (1957) and confirmed by Mulligan (1957) for *A. coronopifolia* supports this relationship. *Ambrosia coronopifolia* may therefore be considered a tetraploid species. *Ambrosia* × *intergradiens* would then be a triploid. Heiser and Whitaker's (1948) report of California material of *A. psilostachya* (Solano Co., Heiser 1966, UC) as having an estimated "n = 50–52" suggested to us that the actual figure might be $n = 54$, i.e., the hexaploid number. Materials kindly collected for us by Mrs. D. A. Beals in Los Angeles Co., California (MICH) were observed in Metaphase I and Metaphase II: a total of 20 estimates ranged from 50 to 56, the average $n = 53$. The exact number may, accordingly, really be $n = 54$. It is worthy of mention at this point that smaller-spored forms also occur in the perennial ragweeds of California, suggesting that tetraploid taxa exist there as well as hexaploid. Three collections (San Diego Co., Palmer 161; Lathrop, Walker 889; and Yuba Co., Howell 28288—all UC) averaged 20.8 microns in diameter of pollen grains, with a range from 18.5–23.3, corresponding closely to the figures given above for *A. coronopifolia*.

On the basis of present knowledge, therefore, we may assume that there are probably at least four polyploid levels in the *A. artemisiifolia-coronopifolia* complex, viz. $2x$ (*artemisiifolia*), $3x$ (*intergradiens*), $4x$ (*coronopifolia* plus this or an additional taxon that grows in California), and $6x$ (*psilostachya*). Where it has been possible to compare them, the levels of polyploidy are matched by corresponding average pollen diameters, viz. 17.6 microns (*artemisiifolia*), 20.5 microns (*coronopifolia*), and 23.0 microns (*psilostachya*). *Ambrosia* × *intergradiens* does not conform with the sequence, but its irregular meiotic conditions and degree of spore abortion are such that the normal process of pollen ontogeny may be disturbed and thus produce the deviation.

It can be concluded that polyploidy has played an important role in the evolution of the *artemisiifolia-coronopifolia* complex of ragweeds. Further knowledge of the evolution of this assemblage will have to be enriched by a survey much broader in scope than the present one. In particular, areas of presumed geographical origin should be sought and investigated. Professor G. L. Stebbins has written (December 18, 1956) that in his opinion the understanding of the relationships of the taxa in this complex will require "a careful study of all the forms occurring in the southwest United States, Mexico, and elsewhere in the American tropics." We might suggest then that the forms that are found in California and in Michigan probably represent peripheral end-point populations derived from an evolutionary matrix that originated in the south. An interesting further possibility was recently indicated by Yuasa (1956) when he pointed out that "since the basic number of chromosomes in Compositae is nine, it is not surprising that the chromosome number of the ragweed [i.e., *A. artemisiifolia*] is $n = 18$." If the original number in these plants was $x = 9$, then the common annual ragweed is a tetraploid species itself; *A. coronopifolia* would have to be interpreted as $8x$; *A.* × *intergradiens* $6x$; and *A. psilostachya* $12x$.

SUMMARY

1. A study of perennial ragweed populations in the state of Michigan was made from standpoints of their distribution, periodicity, habitats, morphological variations, chromosome numbers, and pollen sizes.

2. The known Michigan range of *Ambrosia coronopifolia* was increased by 18 new counties in field studies, bringing the total to 43. The species was found to be frequent across the Upper Peninsula to the north half of the Lower Peninsula and the western part of the southern half. Historical evidence does not favor interpreting it as originally native; in fact, no collections are known prior to 1900.

3. It forms large clones by proliferation from underground parts in disturbed habitats such as roadsides and railways, especially around populated areas. Unlike the annual species (*A. artemisiifolia*) the perennial will invade grassy fields. The substrate is normally sterile, sandy or gravelly soil, in exposed places.

4. *Ambrosia coronopifolia* matures earlier than the annual species by two or three weeks as evidenced by gross morphology and pollen production.

5. Its variations include those of the leaves (lanceolate to deltoid in outline, from coarsely lobed to bipinnatifid, and sessile to short-petiolate), of leaf arrangement (opposite, whorled, and alternate), of plant habit (small and simple, to large and "bushy"), and of spines on the fruit (from unarmed to moderately spiny).

6. Its pollen grains are smaller (20.5 microns in diam.) than previously reported in perennial ragweeds, and an average of 23 per cent of those

tested lacked protoplasts. Its chromosomes number $2n = 72$, and meiosis appears to be normal.

7. An heretofore undescribed perennial ragweed, *A.* × *intergradiens*, hybr. nov., differs from *A. coronopifolia* in hairiness, color, leaf cutting, petiole length, and fruit structure. Its characteristics are intermediate between the latter and the annual *A. artemisiifolia* and it is interpreted as their natural hybrid.

8. The new ragweed is unexpectedly common and a large number of populations have been observed in 15 counties. It grows usually, though not always, in company with the parents.

9. The primary variation of *A.* × *intergradiens* includes characters of hairiness and plant size. One peculiar sterile population was found with wholly pistillate flowers.

10. The pistillate inflorescences average 3 flowers per axil and are thus intermediate between the parents. However, only 16 per cent of the flowers matured normal-appearing fruits, indicating low fertility.

11. Pollen grain diameter of *A.* × *intergradiens* is greater (21.8 microns) than either parent, but the variation is twice that of the parents. Over half of the grains appear to be inviable. The chromosomes number $2n = 54$, but meiosis is irregular with many univalents and a few trivalents at Metaphase I, and with a large number of figures showing lagging of chromosomes.

12. Pollen size of various ragweeds is discussed in relation to polyploid levels: there is a direct correlation. *Ambrosia artemisiifolia* is interpreted as a diploid, *A. coronopifolia* a tetraploid, and *A. psilostachya*, a hexaploid, based on $x = 18$. *Ambrosia* × *intergradiens* is a triploid, but its pollen size does not conform, probably because of irregularities due to its immediate hybrid origin.

13. A really comprehensive knowledge of this complex must entail studies in warmer regions in southern U. S. and Mexico. The primitive members of the complex may have $n = 9$ chromosomes.

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